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Author(s): O. W. Van Auken

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SHRUB INVASIONS OF NORTH AMERICAN SEMIARID GRASSLANDS

O. W. Van Auken

*Division of Life Sciences, University of Texas at San Antonio, San Antonio,
Texas 78249-0662; e-mail: ovanauken@utsa.edu*

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■ **Abstract** The composition and structure of the semiarid or desert grasslands of southwestern North America have changed over the past 150 y. Brushy or woody species in these communities have increased in density and cover. This increase in density of woody species is called brush encroachment because most of these species have been present in these communities at lower densities for thousands of years. The brushy or woody species were not introduced from other continents or from great distances. They are indigenous species that have increased in density or cover because of changes in local abiotic or biotic conditions. The brushy and woody plants are not the cause of these changes, but their increase is the result of other factors. The causes of changes that have led to the present woody-brushy composition of these semiarid grasslands has been difficult to determine. Warming of the climate seems to be a background condition, but the driving force seems to be chronic, high levels of herbivory by domestic animals. This herbivory has reduced the aboveground grass biomass, leading to the reduction of fine fuel and a concomitant reduction or complete elimination of grassland fires. This combination of factors favors the encroachment, establishment, survival and growth of woody plants. Less competition from grasses, dispersal of seeds of woody plants by domestic animals, and changes in rodent, lagomorph, and insect populations seem to modify the rate of change. Elevated levels of atmospheric CO₂ are not necessary to explain shrub encroachment in these semiarid grasslands. The direction of future change is difficult to predict. The density of brushy and woody plants will probably increase as will the stature and number of species. However, if soil nutrients increase, woody legumes may be replaced by other brushy or woody species. Reversing the changes that have been going on for 150 y will be a difficult, long-term, and perhaps impossible, task.

INTRODUCTION

Deglaciation has caused major fluctuations in plant populations throughout the world over the past 11,000–12,500 y. Woodlands with spruce, fir, and pine covered much of what is now mixed deciduous forest in the eastern United States (51–53). Subalpine woodlands were found in areas now covered with piñon-juniper

woodlands in the Great Basin (20, 120). Spruce forests or open spruce, pine, birch parkland occurred in areas of tall grass prairie in Kansas and in areas of juniper grassland or savanna in west central New Mexico. Pine parkland was found in what is now short-grass prairie in western Texas and in areas of desert grassland in southeastern Arizona (78, 79, 85, 147, 166).

In the past 150 y, changes and rates of change of plant populations and communities have been unparalleled (42, 56, 132). Most of the recent changes in woody plant populations associated with grasslands or savannas do not appear to have been caused directly by deglaciation nor are they to be considered invasions as suggested by many authors; rather, these phenomena are associated with adjacent communities that have existed for a considerable time (32, 120). In this chapter I examine, not the establishment and growth of newly introduced species of woody plants, but the increase in density or cover of local shrubs and woody species that have been present in the semiarid grasslands of southwestern North America for thousands of years (86, 93, 167, 169). I favor the word encroachment for this phenomenon.

At lower elevations, brushy or woody species usually associated with the Chihuahuan or Sonoran Deserts have increased in density in areas previously covered by semiarid grassland (29, 82). At higher elevations, various species of juniper, previously restricted to rocky outcrops, steep slopes, and shallow soils have spread downslope into grasslands throughout southwestern North America (21, 59, 90, 115, 120, 170, 174). Not all species have moved, however; for example, populations of *Quercus emoryi* that form woodlands above the semiarid grasslands in Arizona and Northern Mexico apparently have not migrated up or down in elevation for many years (173). However, seedling establishment is restricted to the area below the adult tree canopy (69, 173).

Alterations in density of woody plants have been attributed to climate change (29, 82), but in the semiarid grasslands of the southwestern United States, warming would presumably cause juniper to move northward and up in elevation (120). This did not occur, juniper populations seemed to move down in elevation and are affected by reduced grass biomass and a concomitant reduction in fire frequency (21, 32, 90, 118). Recent climatic or precipitation changes do not seem connected to these vegetation alterations in the semiarid grasslands (8). Anthropogenic forces have apparently caused most of the recent changes in semiarid grasslands either directly or indirectly. The process is known by a number of names, including desertification, shrub invasion, woody plant invasion, and bush or brush encroachment (2, 4, 5, 109, 115, 136, 141, 142, 144) and has occurred throughout the world (1, 2, 4, 7, 21, 29, 34, 77, 81, 82, 120, 141, 142, 144, 150, 164, 168).

AREA OF STUDY

Semiarid grasslands or desert grasslands are found in the basins and valleys of southwestern North America as well as on outwash plains (bajadas) and on the lower foothills (24, 25, 30, 55, 98, 109, 142). Similar vegetation regions occur throughout the world; among them are the Espinal and some parts of the Chaco

in Argentina (151), the veld and some savanna types in southern Africa (30, 44), arid parts of northwestern India (44, 122), the acacia shrublands and semiarid low woodlands between the forests of the southeastern part of Australia, and the interior continental deserts of Australia (13, 63, 124, 130).

The semiarid grasslands of southwestern North America are extensive but discontinuous (24, 25, 30, 55, 98, 109, 142). In the north, they extended from northwest of Dallas in northern Texas, across southern New Mexico, to northwest of Phoenix and west of Tucson in southern Arizona (approximately 35° N 98° W to 31° N 111° W). In the south, they extended from west of Veracruz to northeast of Colima, Mexico (approximately 18° N 96° W to 19° N 104° W). These semiarid regions usually occur at elevations between 1100 and 2500 m. Rainfall may average 230 mm per year in the north to as much as 600 mm per year at higher elevations in the south. Approximately 50% of the rain falls between May and October in western Arizona, 75% during this time period in western Texas, and as much as 90% during this time period in central Mexico (109). Mean annual temperature ranges from 13°C to 16°C with fewer than 75 d with freezing temperatures (149); evaporation rates are high (142). Plant productivity in semiarid grasslands is the lowest of all North American grasslands, probably because of low and variable rainfall, high evapotranspiration, and shallow soil (109, 119, 142, 149). Aboveground net primary production values as low as 43 g m⁻² yr⁻¹ have been reported, but total plant production is thought to be about 250–350 g m⁻² yr⁻¹ (109).

Soils are mostly Aridisols, Mollisols, or Entisols (9, 105). Most are usually shallow, but they may be deep in places. They include sandy outwash material with little horizon development to very old, deep soils with well-developed profiles. Deeper soils may have clay-loam to clay subsoils and well-developed calcic horizons. Most of these semiarid grassland soils have less organic material than other grassland soils (142). The surface and subsurface properties of the soils, especially the distribution of water and the capacity to hold water, determine to a large extent the kind of plants found on the surface (107, 108).

Many different names have been used to describe the semiarid grasslands of the southwestern United States and central and northern Mexico, including, Desert grassland (55, 110), semidesert grassland (25), Chihuahuan desert grassland, Sonoran desert grassland, high desert bunchgrass, and high desert sod grass (142), and others (30). In Mexico, the names of the communities include pastizal, mesquital, matorral crasicaule, matorral desértico rosetófilo, and the matorral desértico micrófilo (138, 142).

Much of the area listed above as semiarid grassland has also been described as savanna, including various types of piñon-juniper savanna, southwestern oak savanna, and mesquite savanna (115), or as an ecotone (55, 142). Much of the biology and ecology of savanna species interactions have been considered recently (144). In the east, the semiarid grasslands merge with or interdigitate with the Chihuahuan Desert shrublands at elevations of about 1000 m and where precipitation falls to about 250 mm per year. In the northeast, the semiarid grassland blends into the short grass prairie, but the boundaries are vague. In the west, the semiarid grasslands merge with or interdigitate with the Sonoran Desert shrublands at low

elevations and where precipitation is reduced; whereas at elevations of more than approximately 1750 m in the United States and more than 2500 m in Mexico, they merge with or interdigitate with evergreen-oak savanna, woodland, or chaparral (107, 142).

HISTORICAL BACKGROUND

Reports of increased density of brushy or woody plants in the semiarid grasslands of southwestern North America are not new. The timing of encroachment of woody plants in Arizona has been well documented and seems to be associated with large-scale cattle ranching in the 1870s and fire exclusion (6, 7). The documentation is also fairly good for New Mexico and Texas, although the process may have started sooner (2, 55, 86). However, all of these changes have occurred with a backdrop of climate change, which makes sorting out causal forces very difficult.

Some woody plants that were introduced into southwestern North America and are now apparently well established may be found in widespread areas whereas others are quite localized. *Euryops multifidus* (resin bush), a South African shrub that was introduced into southern Arizona in 1938 (107), is not eaten by domestic or native herbivores and continues to spread. It grows on hillsides and mesas in the semiarid grasslands, and native grasses and woody plants have disappeared from areas where it is found. Several species of *Tamarix* (salt cedar or Tamarisk) have been introduced into southwestern North America from the Mediterranean region, the Middle East or Africa (49). The two most widespread species, *Tamarix chinensis* and *T. gallica*, which seem to have the greatest densities (86, 152), occur in riparian zones and in salt flats and other salinized, wet soils associated with the semiarid grasslands but not in the grasslands themselves. *Elaeagnus angustifolia* (Russian olive) is also a widely distributed, introduced small tree that is found in riparian habitats associated with semiarid grasslands.

A number of herbaceous invaders from the Middle East and Africa have also been introduced into the southwestern semiarid grasslands (12, 23, 123). These heavily grazed, disturbed habitats are more likely to be invaded than similar non-disturbed habitats (10), and the invaders are usually introduced annuals from the families Poaceae, Asteraceae, and Brassicaceae (6, 30, 31, 100, 112, 131, 137, 152). In southwestern North America, approximately 10% of the local floras are established, non-native species, but it is unknown how many seeds of non-native species arrive, germinate, grow, die and never establish a viable population (60, 95, 103).

ENCROACHING SPECIES

It is difficult to estimate the area that has changed from semiarid grassland to shrubland in southwestern North America and the area occupied by the major encroaching species. Approximately 60 million ha are estimated (77, 86), but this

area is larger than that estimated for the semiarid grasslands of southwestern North America (98). One cause of this apparent paradox is that more than one species of woody plant is found in the same area (77), and another is that some species of encroaching woody plants are found outside the semiarid grasslands but these areas have not been differentiated. The third cause is that some areas have a high density or cover of the woody plant, others are moderate, and some are light. Nonetheless, it seems that the composition and structure of most, if not all, semiarid southwestern grasslands has been changed by the encroachment of one or more shrubby or woody species.

Prosopis (mesquite, possibly *P. glandulosa*, *P. velutina*, *P. torreyana* or *P. juliflora*, depending on the systematics and location) is the dominant woody plant on more than 38 million ha of what has been considered semiarid southwestern grasslands. *Larrea tridentata* (creosotebush) is the dominant shrub on more than 19 million ha of similar grasslands. Other shrubs, small trees, or succulents that have increased in density and area can be locally important, but individually do not cover nearly the same area as do *Prosopis* and *Larrea*. They include various species of *Acacia*, *Yucca*, *Flourensia*, *Haplopappus*, *Opuntia*, *Gutierrezia*, *Juniperus*, and *Quercus* (55, 77, 86, 142).

CAUSES OF ENCROACHMENT

The causes of shrub or woody plant encroachment in semiarid grasslands throughout the world have been much debated. Most often cited as reasons are climate change, chronic high levels of herbivory, change in fire frequency, changes in grass competitive ability, spread of seed by livestock, small mammal populations, elevated levels of CO₂, and combinations of these factors (2–4, 6, 7, 18, 37, 64, 86, 121, 125, 134, 142, 158, 166, 171). Most of the changes in woody plant density have been associated with the introduction of cattle into these grasslands (3, 6, 7, 11, 127, 129).

Some small amount of herbivory is tolerated by plants without noticeable changes in productivity, biomass, growth, or reproduction, but higher levels result in depression or reduction of these factors (2, 14, 68, 80, 84, 99). The stimulation of plant growth directly by herbivory and benefits of herbivory to plants seems minimal and probably rarely occur, but these topics have received considerable attention in the literature (16, 17, 22, 58, 113, 128). Rather, chronic high levels of herbivory seem to negatively affect plants and are the dominant reasons for the encroachment of shrubs and other woody plants into the semiarid grasslands and for changes in woody plant density (3, 6, 7, 11, 127, 129). The introduction of cattle seems to be the primary factor in the conversion of semiarid grasslands into shrublands or woodlands, but the mechanisms involved are still not well understood, and the rates, dynamics, patterns, and successional processes are not well defined.

GLOBAL CHANGE

We are currently in an interglacial period that started about 12,500 y ago. The climate has been warming since the most recent glacial period ended (88, 111). Apparently plant communities migrate as the climate warms or cools. During the current warming trend, in what are now the semiarid grasslands or desert grasslands of southwestern North America, pine parkland and juniper woodland or savanna moved mostly in a northern direction or up in elevation to their approximate current location. Changes in the populations of plants and animals of the communities of the American southwest have been pieced together from pollen records and fossil packrat middens (20, 104, 120, 166). There does not seem to be conclusive evidence that changes in precipitation patterns or temperature in southwestern North America since the 1870s are linked to recent shrub or woody plant encroachment in the semiarid grasslands. The unevenness of this encroachment, especially for *Prosopis*, and dramatic differences in density in adjacent fenced, edaphically similar areas would seem to rule out large scale climatic influences as the major cause of woody plant increases (8). It has also been proposed that the rising level of atmospheric CO₂ is the cause of shrub encroachment (87, 92, 106, 133). This hypothesis could account for the synchronous, widespread encroachment of shrubs and other woody plants into semiarid grasslands and savannas throughout the world. It is based on observations that most woody plants have the C₃ photosynthetic pathway and in the semiarid grasslands, the grasses that are being replaced have the C₄ photosynthetic pathway.

Plants with the C₃ photosynthetic pathway have a growth advantage at higher levels of CO₂ compared to plants with the C₄ photosynthetic pathway. However, there are some difficulties with this hypothesis (3). Quantum yields, photosynthesis rates, and water-use efficiencies are comparable for a variety of C₃ and C₄ species at current levels of CO₂. Many C₄ grasses are more responsive to increased levels of CO₂ than previously supposed. The replacement of C₃ grasses by encroaching C₃ woody shrubs in the cold deserts is not explained by the hypothesis of elevated CO₂. Fences reduce the encroachment of C₃ woody shrubs in edaphically similar areas with C₄ grasses. Shifts in populations of C₄ grasses to C₃ grasses in these same areas have not occurred. There is a temporal disparity between the time of the greatest increase in CO₂ which occurred after approximately 1910 and the encroachment of woody plants that had by this time in many areas already started or occurred (3). Many shifts in dominance of woody plants and grasses during the Holocene do not appear to be related to elevated levels of CO₂. Finally, not all studies have shown a CO₂ fertilizer effect, suggesting other limitations or constraints.

COMPETITION

The importance of competition between grasses and woody species has been demonstrated in many arid and semiarid communities (41, 65). In addition, interactions between and among species are known to be important in determining

community structure and function. Competition between species is considered one of the major factors determining community characteristics (75, 76, 80), but it is one of several factors (39, 40, 135, 173) and is continually debated (72–74, 155). Competition has been reported in many studies (143), but intraspecific competition was as strong as interspecific competition in 75% of the examples (48). However, the growth of plants in arid and semiarid communities is at least partially controlled by interference from neighbors (41, 65, 101, 102), and this growth can be modified by herbivory (37, 141, 158).

Changes in competition between grasses and woody plants are implicated in the encroachment of woody plants into semiarid grasslands (176), where competition is primarily belowground (36, 158, 176). Because of the low stature of the plants, relatively low plant density, high belowground biomass, and high root:shoot ratios (36, 158, 176) competitive ability of plants in these communities may depend on root biomass, root density, root branching, root radius, root hair characteristics, mycorrhizae, timing of growth, or interactions with other soil organisms (41, 163, 165). Competition in these semiarid grasslands seems to change depending on the species and environmental conditions. Grasses inhibit the woody species most during the germination, establishment, and early growth of the woody plants (37, 158, 163). However, the interaction seems to be reversed once the woody plant roots are below the root zone of the grasses and the woody plant shoot is above the shoot zone of the grasses (19, 28, 35, 97).

Probably the best-studied woody species in these semiarid grasslands are *Prosopis* (mesquite, *Prosopis glandulosa* and other species) and *Acacia* (*Acacia smallii* and other species). Aboveground, belowground, and total dry mass of *Prosopis glandulosa* was reduced or suppressed when it was grown in the greenhouse with some C₄ grasses (36, 157, 159, 160, 163) or when it was grown in the field with C₄ grasses (37, 62, 71, 158). However, several studies did not show growth inhibition (27, 28), probably because of lower levels of herbaceous biomass or site-specific factors. Similar trends have been shown for *Acacia smallii* in greenhouse competition studies with C₃ and C₄ grasses and in the field (43, 161, 162).

Although high density or biomass of grass reduces germination, survival, and growth of woody seedlings, some seedlings survive (27, 28, 158, 163; cf 37). Despite suppressed growth, some of these seedlings would finally escape the grass zone of suppression and ultimately convert the grassland into shrubland or woodland. If, for example, one woody plant ha⁻¹ produced ten survivors ha⁻¹ y⁻¹, in 100 y the density of that species of woody plant would be 1000 plants ha⁻¹, the grassland would have become a shrubland or woodland.

FIRE

Periodic burning is required to control or reduce the establishment and growth of woody plants in most if not all grasslands (47, 177). Fire interacts with other factors such as topography, soil, herbivores, and amount of herbaceous fuel to determine

the nature, density, and location of woody plants in a landscape (77, 86, 117, 177). The occurrence and frequency of fires is linked to climate. In higher elevation forest communities of the southwestern United States, fire occurrence is determined by climatic patterns associated with Southern Oscillations (high phase-La Niña, low phase-El Niño) (154). Large fires usually occur after dry springs (La Niña) and smaller fires follow wet springs (El Niño). The same is probably true for the lower elevation semiarid grasslands in the American southwest.

Fire frequency in the semiarid grasslands has decreased in the past 150 y, as has fire size, while the size and density of the woody plants has increased and biomass of grass has decreased (6). There is historical evidence of fires in these semiarid grasslands from the earliest travelers and European settlers (6, 86, 89), although some authors do not think there was ever enough fuel in these semiarid grasslands to carry an extensive fire or do not agree with the evidence (29, 55, 82). Most changes in the composition of the semiarid grasslands in southeastern Arizona, and probably in New Mexico and western Texas as well, occurred after the beginning of large-scale cattle ranching and fire exclusion in the 1870s (6, 7, 86). Today, wild-fires are rare. High densities of woody plants, low amounts of fuel, and extensive grassland fragmentation seem to be the cause.

The seedlings of many shrubs and other woody plants of the semiarid grasslands are sensitive to fire (117). Some will not resprout if their tops are killed (32), and others are susceptible to fire mortality until reaching an appreciable size (71). If these plants do not produce seeds before they are 10 y of age, then a fire return time of 10 y or less would keep these semiarid grasslands relatively free of woody plants (117). Fire-tolerant species would be suppressed by recurring fires and remain in the grassland at a small size (2). However, with a reduction of the fine fuel load by heavy and constant herbivory, fire frequencies would decrease. Further increases in woody plant cover and density would follow.

HERBIVORY

Herbivores may reduce the growth of individual plants by damaging the leaves, stems, or roots (14, 80, 99). Damage to plants by herbivores is determined by the timing of the encounter, location of the tissue eaten, amount of tissue eaten, and frequency of attack (50). By damaging plant parts, herbivores may alter a plant's ability to obtain resources or selectively eliminate a plant as a competitor, and thereby influence the outcome of species interactions (50, 65, 99). Furthermore, herbivory can increase the number of gaps present in the cover of these semiarid grassland communities, reduce the aboveground and belowground grass biomass, modify the pattern of resource availability, and alter biomass allocation (37, 38, 45, 46, 54, 146, 158). Therefore, at the population level, damage to individual plants by removal of biomass may lead to changes in plant abundance and distribution through alteration in fecundity or ability to regrow

or through changes in mortality (50, 80). The ability of a plant to regrow after encounters with herbivores is usually reduced, and regrowth of grasses following removal of aboveground parts is usually associated with reductions in belowground growth and biomass (54, 145, 163; see however, 18, 22, 58, 113, 114, 128).

In the semiarid grasslands of the American southwest, brush encroachment has been coincident with or been preceded by development of the livestock industry (2, 3, 6, 7). Alterations in the grass species composition as well as reductions in herbaceous plant basal area, density, and aboveground and belowground biomass accompany chronic high levels of livestock grazing (84). Herbivory at low density and frequency may cause little change in a grassland community, but at high density and frequency, it can alter grassland composition, changing it to a shrubland or woodland (2).

If only grasses are consumed by herbivores, they may be at a disadvantage in their ability to interact with other plant species. If, on the other hand, browsers consume the shrubs or woody plants, the woody plants will be at a disadvantage (156). In systems in which woody plants are browsed, woody plant stature remains small and density remains static, but if the browsers are removed, woody plant size and density increase (66). Grazers and browsers in African grasslands and savannas exert a major influence on distribution and abundance of woody plants (15, 57, 153, 178). In the grasslands of central and southwestern North America, defoliation of woody seedlings by rodents, lagomorphs, and insects is an important source of mortality, particularly for *Prosopis glandulosa* (26, 70, 71, 83, 116, 126, 148). The black-tailed prairie dog, *Cynomys ludovicianus*, consumes seeds, pods, and seedlings of *Prosopis glandulosa* and maintains its colony's surface clear of seedlings and saplings (171, 172). Extensive anthropogenic eradication of prairie dogs and reduction of colonies by 98% in the early 1900s may have removed an important constraint to establishment of woody plants over a large area of the American southwest. However, this eradication apparently occurred after extensive encroachment of *Prosopis glandulosa* into many semiarid grasslands (6, 29, 55, 82).

SPREAD OF SEED

One of the theories concerning the maintenance of grasslands free of shrubs or woody plants during most of the Holocene was that dispersal of seeds of woody plants into grasslands was low because of a limited number seed dispersers. Some large and small mammals, including domestic livestock, feed on the fruit of woody plants and act as seed dispersal agents (27, 28, 96, 175). *Prosopis glandulosa*, a native legume, has a thick seed coat that requires scarification, which occurs during mastication; the seed survives passage through the gut of cattle and various native species (28, 96). The introduction of domestic herbivores may have increased the

dispersal of *P. glandulosa* and other woody plant seeds, but many native herbivores could and probably still do the same thing (28, 96). In fact, *Prosopis* and other woody plants were present in many semiarid grasslands prior to increases in domestic herbivores, although plant density and probably stature have increased (8). These increases in woody plant density would not seem to require long-distance seed dispersal by domestic herbivores and could have been dispersed as far by native species.

MECHANISMS OF SHRUB OR WOODY PLANT ENCROACHMENT

The first and possibly the most critical factor causing woody plant encroachment is chronic high levels of herbivory by domestic animals. This causes a reduction of the aboveground grass biomass and of the light, fluffy fuel needed for grassland fires, thereby reducing fire frequency. With a lack of periodic fires, shrubs and other woody plants have a growth advantage over the grasses. Reducing aboveground and belowground biomass of grass through chronic high levels of herbivory by domestic ungulates would decrease the competitive ability of the grass (35, 37, 145, 158). At the same time, decreased grass cover would cause increased runoff and erosion leading to increases in temporal and spatial heterogeneity for soil resources, especially water, nitrogen, and probably phosphate (139–141). Low soil-nitrogen levels would favor establishment of species that have low soil nitrogen requirements, such as *Larrea tridentate* and many leguminous shrubs including acacias, paloverdes, and mesquite (61, 91). With the growth of woody plants, resources are partitioned differently. Clumps of shrubs or woody plants concentrate soil resources in many arid and semiarid communities; these areas are termed resource islands (4, 33, 34, 67, 94, 141). Soil resources are recycled in these resource islands, making them favored sites for germination and growth of woody plants that may establish readily, thereby making it more difficult for grass reestablishment. Cyclic droughts would seem to favor the deeper-rooted woody plants, but recent changes in the rainfall regime do not seem to be a cause of establishment. Past changes in temperature and atmospheric CO₂ do not appear to be the main cause of the rapid, recent shift in woody plant populations, but continued increases in temperature and atmospheric CO₂ concentration will probably play some future role. It is difficult to evaluate the past role of small native mammals and insects in reducing the survival and growth of brushy and woody plant seedlings thereby maintaining the grassland habitat. It would seem that their effects would not be uniform, but important in some areas. Shifts in plant populations and soil resources would reduce some populations of animals that feed on the seedlings of woody plants that could change woody seedling survival and further alter community structure.

CONCLUSIONS

The semiarid grasslands of southwestern North America have changed dramatically over the last 150 y. These grassland communities have not been invaded by non-native bushy, shrubby, or woody species. The process is encroachment and the species are native. Encroachment of native woody species has changed the appearance and structure of many of these former semiarid grasslands to shrublands, brushlands, or woodlands. *Prosopis* (mesquite) has probably increased in density and cover over a larger area than any other species. Although some authors have attributed the encroachment of shrubs or woody plants into the semiarid grasslands to one factor, often climate change, most recent studies have suggested an interaction of several factors. The major cause of the encroachment of these woody species seems to be the reduction of grass biomass (fine fuel) by chronic high levels of domestic herbivory coupled to a reduction of grassland fires, which would have killed or suppressed the woody plants to the advantage of the grasses. The role of plant competition and the spread of seeds by introduced domestic herbivores seem to be secondary and probably modified the rate of change. The role of many small native mammals and insects that consume woody plant seedlings seems to be secondary and possibly localized. Secondary factors probably modified the rate of change, rather than causing the change. Thus, the brushy and woody plants are not the cause of the changes in these semiarid grasslands as is so often presumed, but they are the result of the effect of changes of other factors on the species in these grassland communities.

The stature and composition of these communities has changed dramatically over the past 150 y and will continue to change in the future. Although chronic high levels of herbivory by domestic animals seems to have been the driving force behind the changes in stature and composition of these semiarid grasslands, the direction of future change or trends is difficult to predict. All of the above factors will probably continue to interact to regulate community composition and structure. The density of shrubby and woody plants will probably increase with some increase in stature and number of species. However, if soil nutrients increase, the woody legumes may be replaced by other shrubby or woody species. Reversing the trend or changes that have been going on for 150 y will be a difficult, probably long-term process, and possibly impossible task.

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LITERATURE CITED

1. Adamoli J, Sennhauser E, Acero JM, Rescia A. 1990. Stress and disturbance: vegetation in the dry Chaco region of Argentina. *J. Biogeogr.* 17:491–500
2. Archer S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In *Ecological Implications of Livestock Herbivory in the West*, ed. M Vavra, WA Laycock, RD Pieper, pp. 13–69. Denver: Soc. Range Manage.
3. Archer S, Schimel DS, Holland EA. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Clim. Change* 29:91–9
4. Archer S, Scifres C, Bassham CR, Maggion R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Monogr.* 52: 111–27
5. Archer SR. 1989. Have southern Texas savannas been converted to woodlands in recent history? *Am. Nat.* 134:545–61
6. Bahre CJ. 1995. Human impacts on the grasslands of southeastern Arizona. See Ref. 110, pp. 230–64
7. Bahre CJ. 1991. *A Legacy of Change: Historic Human Impact on Vegetation of the Arizona Borderlands*. Tucson: Univ. Ariz. Press
8. Bahre CJ, Shelton ML. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *J. Biogeogr.* 20:489–504
9. Bailey RG. 1978. *Description of the Ecoregions of the United States*. Ogden, UT: US Dep. Agric., For. Serv., Intermountain Region
10. Baker HG. 1986. Patterns of plant invasion in North America. See Ref. 20a, pp. 44–57
11. Bartolome JW. 1993. Application of herbivory optimization theory to rangelands of the western United States. *Ecol. Appl.* 3:27–9
12. Bazzaz FA. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. See Ref. 20a, pp. 96–110
13. Beadle NCW. 1981. *The Vegetation of Australia*. New York: Gustav Fischer Verlag
14. Belsky AJ. 1986. Does herbivory benefit plants? A review of the evidence. *Am. Nat.* 127:870–92
15. Belsky AJ. 1984. Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *Africa J. Ecol.* 22:271–9
16. Belsky AJ. 1996. Viewpoint: Western juniper expansion: Is it a threat to arid northwestern ecosystems? *J. Range Manage.* 49:53–9
17. Belsky AJ, Blumenthal DM. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conserv. Biol.* 11:315–27
18. Belsky AJ, Matzke A, Uselman S. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. *J. Soil Water Conserv.* 54:419–31
19. Berendse FA. 1981. Competition between plant populations with different rooting depths. II. Pot experiments. *Oecologia* 48:334–41
20. Betancourt JL, Van Devender TR, Martin PS. 1990. Synthesis and prospectus. In *Packrat Middens: The Last 40,000 Years of Biotic Change*, ed. JL Betancourt, TR Van Devender, PS Martin, pp. 435–47. Tucson: Univ. Ariz. Press
- 20a. Billings WD, Golley F, Lange OL, Olson JS, Remmert H, ed. 1986. *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag

21. Blackburn WH, Tueller PT. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. *Ecol. Monogr.* 51:841–8
22. Briske D. 1993. Grazing optimization: a plea for a balanced perspective. *Ecol. Appl.* 3:24–6
23. Brock JH, Wade M, Pysek P, Green D, eds. 1997. *Plant Invasions: Studies from North America and Europe*. Leiden: Backhuys
24. Brown DE. 1982. Plains and Great Basin grassland. In *Biotic Communities of the American Southwest—United States and Mexico*, ed. DE Brown. *Desert Plants* 4:115–21
25. Brown DE. 1982. Semidesert grassland. In *Biotic Communities of the American Southwest—United States and Mexico*, ed. DE Brown. *Desert Plants* 4:123–31
26. Brown JH, Heske EJ. 1990. Control of a desert grassland transition by a keystone rodent guild. *Science* 250:1705–7
27. Brown JR, Archer S. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80:2385–96
28. Brown JR, Archer S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80:19–26
29. Buffington LC, Herbel CH. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecol. Monogr.* 35:139–64
30. Burgess TL. 1995. Desert grassland, mixed shrub savanna, shrub steppe, or semidesert shrub? The dilemma of coexisting growth forms. See Ref. 110, pp. 31–67
31. Burgess TL, Bowers JE, Turner RM. 1991. Exotic plants at the Desert Laboratory, Tucson, Arizona. *Madrono* 38:96–114
32. Burkhardt JW, Tisdale EW. 1976. Causes of juniper invasion in southwestern Idaho. *Ecology* 57:472–84
33. Burquez A, de los Angeles-Quintana M. 1994. Islands of diversity: ironwood ecology and the richness of perennials in a Sonoran Desert biological reserve. In *Ironwood: An Ecological and Cultural Keystone on the Sonoran Desert*, ed. GP Nabhan, JL Carr, pp. 9–27. Tucson: Conserv. Int.
34. Bush JK, Van Auken OW. 1986. Changes in nitrogen, carbon, and other surface soil properties during secondary succession. *Soil Sci. Soc. Am. J.* 50:1597–1601
35. Bush JK, Van Auken OW. 1991. Importance of time of germination and soil depth on growth of *Prosopis glandulosa* (Leguminosae) seedlings in the presence of a C₄ grass. *Am. J. Bot.* 78:1732–39
36. Bush JK, Van Auken OW. 1989. Soil resource levels and competition between a woody and herbaceous species. *Bull. Torr. Bot. Club* 116:22–30
37. Bush JK, Van Auken OW. 1995. Woody plant growth related to planting time and clipping of a C₄ grass. *Ecology* 76:1603–9
38. Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14–24
39. Callaway FM, DeLucia EH, Moore D, Nowak R, Schlesinger WH. 1996. Competition and facilitation: contrasting effects of *Artemisa tridentata* on desert vs. montane pines. *Ecology* 77:2130–41
40. Callaway RM. 1995. Positive interactions among plants. *Bot. Rev.* 61:306–49
41. Casper BB, Jackson RB. 1997. Plant competition underground. *Annu. Rev. Ecol. Syst.* 28:545–70
42. Chapin FS III, Sala OE, Burke IC, Grime JP, Hooper DU, et al. 1998. Ecosystem consequences of changing biodiversity. *BioScience* 48:45–52
43. Cohn EJ, Van Auken OW, Bush JK. 1989. Competitive interactions between *Cynodon dactylon* and *Acacia smallii* seedlings

- at different nutrient levels. *Am. Midl. Nat.* 121:265–72
44. Cole MM. 1986. *The Savannas: Biogeography and Geobotany*. New York: Academic Press
 45. Collins SL. 1987. Interaction of disturbances in tall grass prairie: a field experiment. *Ecology* 68:1243–50
 46. Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280:745–47
 47. Collins SL, Wallace LL. 1990. *Fire in North American Tallgrass Prairies*. Norman, OK: Univ. Okla. Press
 48. Connell JH. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122:661–96
 49. Correll DS, Johnston MC. 1970. *Manual of the Vascular Plants of Texas*. Renner, TX: Texas Res. Foun.
 50. Crawley MJ. 1997. Plant-herbivore dynamics. In *Plant Ecology*, ed. MJ Crawley, pp. 401–74. Oxford: Blackwell Sci.
 51. Davis MB. 1981. Quaternary history and the stability of forest communities. In *Forest Succession: Concepts and Applications*, ed. DC West, HH Shugart, DB Botkin, pp. 132–53. New York: Springer-Verlag
 52. Delcourt PA, Delcourt HR. 1981. Vegetation maps for the eastern United States: 40,000 yr B. P. to present. In *Geobotany II*, ed. RC Romans, pp. 123–65. New York: Plenum
 53. Delcourt PA, Delcourt HR, Webb T. 1983. Dynamic plant ecology: the spectrum of vegetation change in space and time. *Q. Sci. Rev.* 1:153–75
 54. Detling JK, Dyer MI, Winn DT. 1979. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia* 41:127–34
 55. Dick-Peddie WA. 1993. *New Mexico Vegetation: Past, Present, and Future*. Albuquerque: Univ. New Mexico Press
 56. Dobson AP, Bradshaw AD, Baker AJM. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* 277:515–22
 57. Dublin HT, Sinclair ARE, McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J. Animal Ecol.* 49:1147–64
 58. Dyer MI, Turner CL, Seastedt TR. 1993. Herbivory and its consequences. *Ecol. Appl.* 3:10–16
 59. Eddleman LE. 1987. Establishment and stand development of western juniper in central Oregon. In *Proc. Pinyon-Juniper Conf.*, ed. RL Everett, pp. 255–59. Ogden, UT: US For. Serv. General Tech. Rep. INT-215.
 60. Enserink M. 1999. Biological invaders sweep in. *Science* 285:1834–36
 61. Felker P, Clark PR. 1980. Nitrogen fixation (acetylene reduction) and cross inoculation in 12 *Prosopis* (mesquite) species. *Plant Soil* 57:114–26
 62. Felker P, Smith D, Smith M, Bingham RL, Reyes I. 1984. Evaluation of herbicides for use in transplanting *Leucaena leucocephala* and *Prosopis alba* on semi-arid lands without irrigation. *For. Sci.* 30: 747–55
 63. Fitzpatrick EA, Nix HA. 1970. The climatic factor in Australian grassland ecology. In *Australian Grasslands*, ed. RM Moore, pp. 3–26. Canberra: Aust. Natl. Univ. Press
 64. Fleischner TL. 1994. Ecological costs of livestock grazing in western North America. *Conserv. Biol.* 8:629–44
 65. Fowler NL. 1986. The role of competition in plant communities in arid and semiarid regions. *Annu. Rev. Ecol. Syst.* 17:89–110
 66. Friedel MH. 1985. The population structure and density of central Australian trees and shrubs, and relationships to range condition, rabbit abundance and soil. *Aust. Rang. J.* 7:130–39
 67. Garcia-Moya E, McKell CM. 1970. Contribution of shrubs to the nitrogen economy

- of a desert-wash plant community. *Ecology* 51:81–88
68. Gardener CJ, McIvor JG, Willians J. 1990. Dry tropical rangelands: solving one problem and creating another. *Proc. Ecol. Soc. Aust.* 16:279–86
69. Germain HL, McPherson GR. 1999. Effects of biotic factors on emergence and survival of *Quercus emoryi* at lower tree line. *Ecoscience* 6:92–99
70. Gibbens RP, Havstad KM, Billheimer DD, Herbel CH. 1993. Creosotebush vegetation after 50 years of lagomorph exclusion. *Oecologia* 94:210–17
71. Glendening GE, Paulsen HAJ. 1955. Reproduction and establishment of velvet mesquite as related to invasion of semidesert grasslands. *Tech. Bull., USDA* 1127:1–50
72. Goldberg DE. 1994. Influence of competition at the community level: an experimental version of the null models approach. *Ecology* 75:1503–6
73. Grace JB. 1993. The effects of habitat productivity on competition intensity. *Trends Ecol. Evol.* 8:229–30
74. Grace JB. 1995. On the measurement of plant competition intensity. *Ecology* 76:305–8
75. Grace JB, Tilman D. 1990. *Perspective on Plant Competition*. New York: Academic Press
76. Grime JP. 1979. *Plant Strategies and Vegetation Processes*. New York: Wiley
77. Grover HD, Musick HB. 1990. Shrubland encroachment in southern New Mexico, USA: an analysis of desertification processes in the American southwest. *Clim. Change* 17:305–30
78. Gruger J. 1973. Studies on the vegetation of northeastern Kansas. *Geol. Soc. Am. Bull.* 84:239–50
79. Halfsten U. 1961. Pleistocene development of vegetation and climate in the southern high plains as evidenced by pollen. In *Paleoecology of the Llano Estacado*. Fort Burgwin Research Center Report I, ed. F Wencorff, pp. 59–91. Albuquerque: Univ. New Mexico Press
80. Harper JL. 1977. *Population Biology of Plants*. New York: Academic Press
81. Harrington GN, Wilson AD, Young MD. 1984. *Management of Australia's Rangelands*. Melbourne, Aust.: Commonwealth Sci. Industrial Res. Org.
82. Hastings JR, Turner RM. 1965. *The Changing Mile*. Tucson: Univ. Ariz. Press
83. Havstad KM, Gibbens RP, Knorr CA, Murray LW. 1999. Long-term influences of shrub removal and lagomorph exclusion on Chihuahuan Desert vegetation dynamics. *J. Arid Environ.* 42:155–66
84. Heitschmidt RK, Stuth JW. 1991. *Grazing Management: An Ecological Perspective*. Portland: Timberline
85. Hevly RH, Martin PS. 1961. Geochronology of pluvial Lake Cochise, southern Arizona. I. Pollen analysis of shore deposits. *J. Ariz. Acad. Sci.* 2:24–31
86. Humphrey RR. 1958. The desert grassland: a history of vegetational change and an analysis of causes. *Bot. Rev.* 24:193–252
87. Idso SB. 1992. Shrubland expansion in the American southwest. *Clim. Change* 22: 85–86
88. Imbrie J, Imbrie KP. 1979. *Ice Ages: Solving the Mystery*. Short Hills, NJ: Enslow
89. Inglis JM. 1964. *A History of Vegetation on the Rio Grande Plain*. Austin: Texas Parks Wildlife Dept.
90. Johnsen TN. 1962. One-seed juniper invasion of Northern Arizona grasslands. *Ecol. Monogr.* 32:187–207
91. Johnson HB, Meyeux HS Jr. 1990. *Prosopis glandulosa* and the nitrogen balance of rangeland: extent and occurrence of nodulation. *Oecologia* 84:176–85
92. Johnson HB, Polley HW, Meyeux HS. 1993. Increasing CO₂ and plant-plant interactions: effects on natural vegetation. *Vegetation* 104-105:157–70
93. Johnston MC. 1963. Past and present grasslands of southern Texas and northeastern Mexico. *Ecology* 44:456–66

94. Jurena PN, Van Auken OW. 1998. Woody plant recruitment under canopies of two Acacias in a southwestern Texas shrubland. *Southwest. Nat.* 43:195–203
95. Kaiser J. 1999. Stemming the tide of invading species. *Science* 285:1836–41
96. Kamp BA, Ansley RJ, Tunnell TR. 1998. Survival of mesquite seedlings emerging from cattle and wildlife feces in a semi-arid grassland. *Southwest. Nat.* 43:300–12
97. Knoop WT, Walker BH. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *J. Ecol.* 73:235–53
98. Lauenroth WK. 1979. Grassland primary production: North American grasslands in perspective. In *Perspectives in Grassland Ecology: Results and Applications of the US/IBP Grassland Biome Study*, ed. NR French, pp. 3–24. New York: Springer-Verlag
99. Louda SM, Keeler KH, Holt RD. 1990. Herbivory influences on plant performance and competitive interactions. See Ref. 75, pp. 413–44
100. Mack RN. 1986. Alien plant invasion into the Intermountain West: a case history. See Ref. 20a, pp. 191–213
101. Mahall BE, Callaway RM. 1992. Root communication mechanisms and intra-community distributions of two Mojave desert shrubs. *Ecology* 73:2145–51
102. Mahall BE, Callaway RM. 1991. Root communications among desert shrubs. *Proc. Natl. Acad. Sci.* 88:874–6
103. Malakoff D. 1999. Fighting fire with fire. *Science* 285:1841–43
104. Martin PS. 1999. Deep history and a wilder West. See Ref. 136a, pp. 255–90
105. Martin SC, Reynolds HG. 1973. The Santa Rita Experimental Range: your facility for research on semidesert ecosystems. *J. Ariz. Acad. Sci.* 8:56–67
106. Mayeux HS, Johnson HB, Polley HW. 1991. Global change and vegetation dynamics. In *Noxious Range Weeds*, ed. LF James, JO Evans, MH Ralphs, BJ Sigler, pp. 62–74. Boulder, CO: Westview
107. McAuliffe JR. 1995. Landscape evolution, soil formation, and Arizona's Desert Grassland. See Ref. 110, pp. 100–29
108. McAuliffe JR. 1999. The Sonoran Desert: landscape complexity and ecological diversity. See Ref. 136a, pp. 68–114
109. McClaran MP. 1995. Desert grasslands and grasses. See Ref. 110, pp. 1–30
110. McClaran MP, Van Devender TR, eds. 1995. *The Desert Grassland*. Tucson: Univ. Ariz. Press
111. McDowell PF, Webb T III, Bartlein PJ. 1995. Long-term environmental change. In *Ecological Time Series*, ed. TM Powell, JH Steele, pp. 327–70. New York: Chapman & Hall
112. McLaughlin SP, Bowers JE. 1999. Diversity and affinities of the flora of the Sonoran Floristic Province. See Ref. 136a, pp. 12–35
113. McNaughton SJ. 1993. Grasses and grazers, science and management. *Ecol. Appl.* 3:17–20
114. McNaughton SJ, Banyikwa FF, McNaughton MM. 1998. Root biomass and productivity in a grazing system: the Serengeti. *Ecology* 79:587–92
115. McPherson GR. 1997. *Ecology and Management of North American Savannas*. Tucson: Univ. Ariz. Press
116. McPherson GR. 1993. Effects of herbivory and herb interference on oak establishment in a semi-arid temperate savanna. *J. Veg. Sci.* 4:687–92
117. McPherson GR. 1995. The role of fire in the Desert Grassland. See Ref. 110, pp. 131–51
118. McPherson GR, Wright HW, Wester DB. 1988. Patterns of shrub invasion in semi-arid Texas grasslands. *Am. Midl. Nat.* 120:391–97
119. Milchunas DG, Lauenroth WK. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* 63:327–66

120. Miller RF, Wigand PE. 1994. Holocene changes in semiarid pinyon-juniper woodlands: response to climate, fire, and human activities in the Great Basin. *Bioscience* 44:465–74
121. Milton SJ, Dean WR, du Plessis MA, Siegfried WR. 1994. A conceptual model of arid rangeland degradation. *Bioscience* 44:70–6
122. Misra R. 1983. Indian savannas. In *Tropical Savannas*, ed. F Bourliere, pp. 151–66. New York: Elsevier
123. Mooney HA, Drake JA, eds. 1986. *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag
124. Moore RM, Condon RW, Leigh JH. 1970. Semi-arid woodlands. In *Australian Grasslands*, ed. RM Moore, pp. 228–45. Canberra: Aust. Natl. Univ. Press
125. Neilson RP. 1986. High-resolution climatic analysis and southwest biogeography. *Science* 232:27–34
126. Nilsen ET, Sharifi MR, Virginia RA, Rundel PW. 1987. Phenology of warm desert phreatophytes: seasonal growth and herbivory in *Prosopis glandulosa* var. *torreyana* (honey mesquite). *J. Arid Env.* 13:311–18
127. Noy-Meir I. 1993. Compensating growth of grazed plants and its relevance to the use of rangelands. *Ecol. Appl.* 3:32–4
128. Painter EL, Belsky AJ. 1993. Application of herbivore optimization theory to rangelands of the western United States. *Ecol. Appl.* 3:2–9
129. Patten DT. 1993. Herbivore optimization and overcompensation: Does native herbivory of western rangelands support these theories? *Ecol. Appl.* 3:35–6
130. Perry RA. 1970. Arid shrublands and grasslands. In *Australian Grasslands*, ed. RM Moore, pp. 246–59. Canberra: Aust. Natl. Univ. Press
131. Pimentel D. 1986. Biological invasions of plants and animals in agriculture and forestry. See Ref. 20a, pp. 149–62
132. Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The future of biodiversity. *Science* 269:347–50
133. Polley HW, Johnson HB, Mayeux HS. 1992. Carbon dioxide and water fluxes of C₃ annuals and C₃ and C₄ perennials at subambient CO₂ concentrations. *Funct. Ecol.* 6:693–703
134. Polley HW, Johnson HB, Mayeux HS. 1994. Increasing CO₂: comparative responses of the C₄ grass *Schizachyrium scoparium* and grassland invader *Prosopis*. *Ecology* 75:976–88
135. Pugnaire FI, Haase P, Puigdefabregas J. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77:1420–6
136. Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecol. Monogr.* 69:69–106
- 136a. Robichaux RH, ed. 1999. *Ecology of the Sonoran Desert Plants and Plant Communities*. Tucson: Univ. Ariz. Press
137. Roundy BA, Biedenbender SH. 1995. Revegetation in the Desert Grassland. See Ref. 110, pp. 265–303
138. Rzedowski J. 1978. *Vegetacion de Mexico*. Mexico: Limusa
139. Schlesinger WH, Abrahams AD, Parsons AJ, Wainwright J. 1999. Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: rainfall simulation experiments. *Biogeochemistry* 45:21–34
140. Schlesinger WH, Raikes JA, Hartley AE, Cross AF. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77:364–74
141. Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, et al. 1990. Biological feedbacks in global desertification. *Science* 247:1043–48

142. Schmutz EM, Smith EL, Ogden PR, Cox ML, Klemmedson JO, et al. 1991. Desert grassland. In *Natural Grasslands: Introduction and Western Hemisphere*, ed. RT Coupland, pp. 337–62. Amsterdam: Elsevier
143. Schoener TW. 1983. Field experiments on interspecific competition. *Am. Nat.* 122:240–85
144. Scholes RJ, Archer SR. 1997. Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28:517–44
145. Schuster JL. 1964. Root development of native plants under three grazing intensities. *Ecology* 45:63–70
146. Seagle SJ, McNaughton J, Russ RW. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grassland. *Ecology* 73:1105–23
147. Sears PB, Clisby KH. 1956. San Agustin Plains-Pleistocene climate changes. *Science* 124:537–9
148. Simpson BB. 1977. *Mesquite: Its biology in two desert scrub ecosystems*. Stroudsburg, PA: Dowden, Hutchinson & Ross
149. Sims PL, Singh JS, Lauenroth WK. 1978. The structure and function of the ten western North American grasslands. I. Abiotic and vegetational characteristics. *J. Ecol.* 66:251–85
150. Smith TM, Goodman PS. 1987. Successional dynamics in an *Acacia nilotica*–*Euclea divinorum* savannah in southern Africa. *J. Ecol.* 75:603–10
151. Soriano A. 1979. Distribution of grasses and grasslands in South America. In *Ecology of Grasslands and Bamboolands in the World*, ed. M Numata, pp. 84–91. Boston: Dr. W. Junk
152. Stromberg JC, Gengarelly L, Rogers BF. 1997. Exotic herbaceous species in Arizona's riparian ecosystems. In *Plant Invasions: Studies from North America and Europe*, ed. JH Brock, M Wade, P Pysek, D Green, pp. 45–57. Leiden: Backhuys
153. Stuart-Hill GC. 1992. Effects of elephants and goats on the Kaffrarian succulent thicket on the eastern Cape, South Africa. *J. Appl. Ecol.* 29:699–710
154. Swetnam TW, Betancourt JL. 1990. Fire–southern oscillation relations in the southwestern United States. *Science* 249:1017–20
155. Twolan–Strutt L, Keddy PA. 1996. Above- and belowground competitive intensity in two contrasting wetland plant communities. *Ecology* 77:256–70
156. Van Auken OW. 1994. Changes in competition between a C₄ grass and a woody legume with differential herbivory. *Southwest. Nat.* 39:114–21
157. Van Auken OW, Bush JK. 1988. Competition between *Schizachyrium scoparium* and *Prosopis glandulosa*. *Am. J. Bot.* 75:782–9
158. Van Auken OW, Bush JK. 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. *Ecology* 78:1222–9
159. Van Auken OW, Bush JK. 1990. Importance of grass density and time of planting on *Prosopis glandulosa* seedling growth. *Southwest. Nat.* 35:411–5
160. Van Auken OW, Bush JK. 1987. Influence of plant density on the growth of *Prosopis glandulosa* var. *glandulosa* and *Buchloe dactyloides*. *Bull. Torr. Bot. Club* 114:393–401
161. Van Auken OW, Bush JK. 1991. Influence of shade and herbaceous competition on the seedling growth of two woody species. *Madrono* 38:149–57
162. Van Auken OW, Bush JK. 1990. Interactions of two C₃ and C₄ grasses with seedlings of *Acacia smallii* and *Celtis laevigata*. *Southwest. Nat.* 35:316–21
163. Van Auken OW, Bush JK. 1989. *Prosopis glandulosa* growth: influence of nutrients and simulated grazing of *Bouteloua curtipendula*. *Ecology* 70:512–6
164. Van Auken OW, Bush JK. 1985. Secondary succession on terraces of the San Antonio River. *Bull. Torr. Bot. Club* 112:158–66

-
165. Van Auken OW, Manwaring JH, Caldwell MM. 1992. Effectiveness of phosphate acquisition by juvenile cold-desert perennials from different patterns of fertile-soil microsites. *Oecologia* 91:1–6
166. Van Devender TR. 1995. Desert grassland history: changing climates, evolution, biogeography, and community dynamics. See Ref. 110, pp. 68–99
167. Van Devender TR, Spaulding WG. 1979. Development of vegetation and climate in the southwestern United States. *Science* 204:701–10
168. Van Vegten JA. 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio* 56:3–7
169. Vasek FC. 1980. Creosote bush: long-lived clones in the Mojave Desert. *Am. J. Bot.* 67:246–55
170. Wells PV. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains Region. *Science* 148:246–9
171. Weltzin J, Archer S, Heitschmidt R. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* 78:751–63
172. Weltzin JF, Archer S, Heitschmidt RK. 1998. Defoliation and woody plant (*Prosopis glandulosa*) seedling regeneration: potential vs realized herbivory tolerance. *Plant Ecol.* 138:127–35
173. Weltzin JF, McPherson GR. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecol. Monogr.* 69:513–34
174. West NE. 1984. Successional patterns and productivity potentials of pinyon-juniper ecosystems. In *Developing Strategies for Range Management*, ed. NRCNAS, pp. 1301–32. Boulder, CO: Westview
175. Wilson M. 1993. Mammals as seed-dispersal mutualists in North America. *Oikos* 67:159–76
176. Wilson SD. 1998. Competition between grasses and woody plants. In *Population Biology of Grasses*, ed. GP Cheplick, pp. 231–54. Cambridge, UK: Cambridge Univ. Press
177. Wright HA, Bailey AW. 1980. *Fire Ecology and Prescribed Burning in the Great Plains—A Research Review*. Washington, DC: US Dept. Agric., For. Serv. General Tech. Rep. INT-77
178. Yeaton RI. 1988. Porcupines, fires and the dynamics of the tree layer of the *Burkea africana* savanna. *J. Ecol.* 76:1017–29